A Review of Stock Identification of Haddock, *Melanogrammus aeglefinus*, in the Northwest Atlantic Ocean

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Introduction

Haddock, *Melanogrammus aeglefinus* (Fig. 1), is a commercially important groundfish species of the gadid family that is distributed throughout the northwest Atlantic from Greenland to Cape Hatteras (Bigelow and Schroeder, 1953). This range is effectively divided by the Fundian ("Northeast") and Laurentian Channels, both in excess of 180 m in depth (Fig. 2). Although haddock are demersal, they are rarely found in abundance below 180 m, resulting in the channels acting as barriers to dispersal (Needler, 1930). Haddock are found in cool, temperate waters across the continental shelf and over offshore submerged banks, with major commercial aggregations occurring on the southern Grand Bank, Scotian Shelf, and Georges Bank (Zwanenburg et al., 1992).

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ABSTRACT—Haddock, Melanogrammus aeglefinus, *is a principal commercial species distributed throughout the northwest Atlantic Ocean, with major aggregations occurring on Georges Bank and on the Scotian Shelf. This review examines all available information on stock structure of haddock to evaluate the suitability of current stock units and to investigate areas that require further research. Combined information from tag-recapture, demographic, recruitment, meristic, parasitic, and genetic studies provide evidence for the identification of haddock stocks, with major population divisions occurring between New England, Nova Scotia, and Newfoundland waters. Within each of these major divisions a number of discrete stocks appear to exist, although uncertainty remains in the amount of separation found within each region. Research utilizing more recent stock identification techniques should refine and improve our understanding of haddock stock structure in the northwest Atlantic.*

Historically, haddock has been a key species in terms of abundance and contribution to the commercial fisheries in the northwest Atlantic with peak landings of 249,000 metric tons (t) in 1965 (ICNAF, 1967). In contrast, landings have declined to 24,500 t in 1992 (NAFO, 1995), with most haddock stocks across the region in a depressed condition and the focus of rebuilding plans (Fig. 3) (Murphy and Bishop, 1995; Hurley et al., 1997; Frank et al., 1997; Gavaris and Van Eeckhaute, 1998; Brown[1]).

Beneficial to stock recovery and effective fisheries management is the "stock concept," as recruitment within each stock must sustain each population's catch (Kutkuhn, 1981). In fisheries science, many claim that the most useful definition of a stock is one that has a sound genetic basis because management policies may not achieve long-term conservation goals without the knowledge of the number of noninterbreeding, self-recruiting populations contained within an exploited species distribution (Ovenden, 1990). Similarly, in accordance with the "biological stock

[1] Brown, R. W. 1998. U.S. assessment of the Georges Bank (5Z) haddock stock, 1998. U.S. Dep. Commer, NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., NEFSC Lab. Ref. Doc. 98.

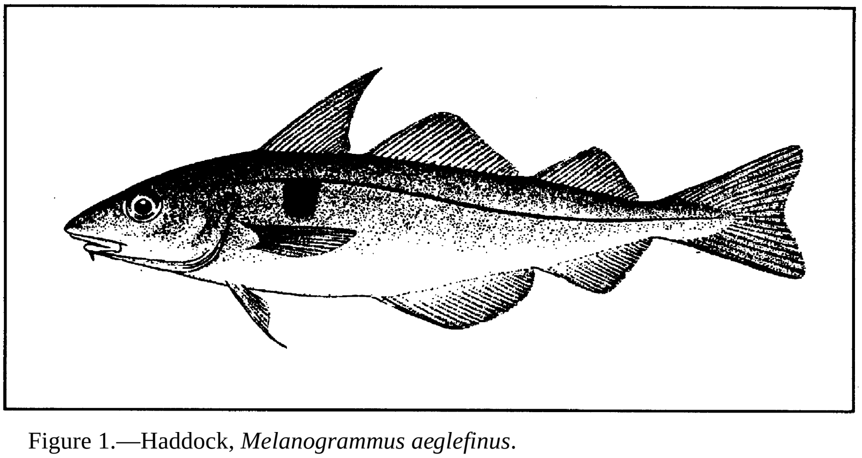

Figure 1.—Haddock, *Melanogrammus aeglefinus*.

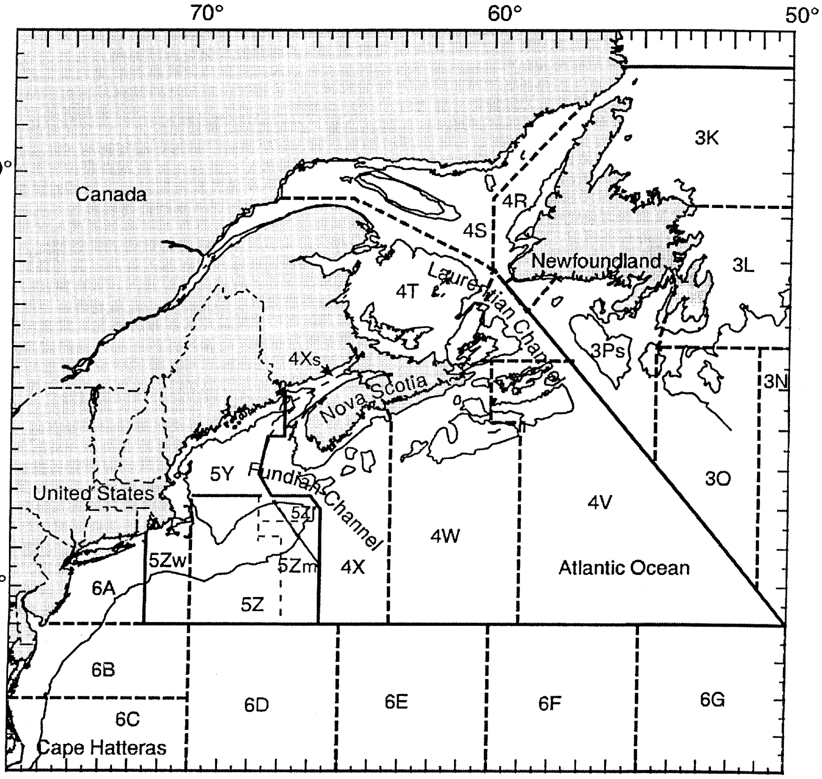

Figure 2.—ICNAF/NAFO scientific and statistical subareas, divisions, and subdivisions of the northwest Atlantic.

concept," fisheries management in the northwest Atlantic has been concerned with the delineation of fishing areas that correspond to geographic ranges of independently reproducing populations (stock distribution areas) (Zwanenburg et al., 1992). Interpretation of stock structure in this review relates to the Ihssen et al. (1981) definition of a stock as "a group of randomly mating, reproductively isolated individuals of a single species with temporal or spatial integrity."

The definition of management units in the northwest Atlantic upon which haddock stocks are assessed and regulated has been based not only on considerations of biological stock structure, but also on considerations of other species and fishery distributions, oceanographic features, submarine topography, political and administrative boundaries, homogeneity of international fisheries participation, and practicalities of data collection and fishery regulation (Halliday and Pinhorn, 1990). In contrast to biological stock units, fisheries management units are geographic areas in which a suite of regulatory measures can be applied to achieve specific management objectives (Gavaris and Van Eeckhaute, 1998). Currently, six stocks are recognized for haddock in the northwest Atlantic: 1) Grand Banks (Div. 3LNO), 2) St. Pierre Bank (Div. 3Ps), 3) Eastern Scotian Shelf and Southern Gulf of St. Lawrence (Div. 4TVW), 4) Western Scotian Shelf (Div. 4X), 5) Georges Bank (Div. 5Zjm - Canada; Div. 5Z - USA), and 6) Gulf of Maine (Div. 5Y) (Fig. 2).

Stock identification studies of haddock in the northwest Atlantic have been conducted since the 1930's, using a variety of approaches including tag-recapture, demographic, recruitment, meristic, parasitic, and genetic techniques. Delineation of haddock stocks has been complicated by seasonal differences in the species' spatial distributions (Zwanenburg et al., 1992) and the limitations associated with individual stock identification methods. This paper reviews the literature on stock identification of haddock in the northwest Atlantic in order to evaluate the suitability of the current management/stock units by using all available biological information, rather than that acquired from a single procedure in isolation. Areas for future research are also discussed.

Stock Identification Techniques

Tag-Recapture

Stock identification of haddock in the Gulf of Maine and Nova Scotian waters was initially determined using tag-recapture methods (Needler, 1930; Schroeder, 1942; McCracken, 1960; Halliday and McCracken, 1970; McKenzie[2]; McCracken[3]). Needler (1930) hypothesized three main stocks of haddock in the northwest Atlantic (New England, Nova Scotia, and Newfoundland) based on divisions of shallow-water areas by the Fundian and Laurentian Channels and movement patterns of the species. Tag-recapture data have indicated that there is little interchange between haddock from New England and Nova Scotian waters (Fig. 4, 5) (Needler, 1930; Schroeder, 1942). However, in the Bay of Fundy, where the two regions are linked by shallow water, some mixing of haddock occurs (Fig. 6) (Needler, 1930; McCracken, 1960; Halliday and McCracken, 1970).

Seasonal migrations have been observed in haddock from both New England and Nova Scotian waters (Needler, 1930; McCracken, 1960; Halliday and McCracken, 1970). Typically, haddock move to inshore shallow waters in spring and to deeper offshore waters throughout winter and late summer (Fig. 6) (Needler, 1930). A large number of local tag-returns a year or more later show that most haddock return to the same locality (Needler, 1930). Tag-recapture data have indicated that a separate seasonally migrating stock exists along the coast of the Gulf of Maine from Jeffreys Ledge to the Bay of

[2] McKenzie, R. A. 1940. The spring haddock "run," Jordan Harbour, N.S. Fish. Res. Board Can., Atl. Prog. Rep. 28:9-13.

[3] McCracken, F. D. 1956. Cod and haddock tagging off Lockeport, N.S. Fish. Res. Board Can., Atl. Prog. Rep. 64:10-15.

Fundy (Div. 5Y/4Xs) (Schroeder, 1942; Grosslein, 1962). McCracken (1960) observed a northward migration of haddock in the Gulf of Maine in spring, followed by a return migration in winter, with some recaptures on Georges Bank and across the Bay of Fundy. Likewise, in waters of eastern Nova Scotia there is evidence that haddock summer in the north and winter in the south, with a seasonal migration in and out of the Gulf of St. Lawrence (Div. 4TVW), although these patterns were based almost exclusively on the results of inshore tagging studies and recaptures from mainly inshore fisheries (Fig. 4) (Needler, 1930). Tag-recapture data also suggest that much of the stock present in summer along the coast of western Nova Scotia (Div. 4X) move offshore in autumn to Browns Bank and return the following spring (Fig. 6) (Halliday and McCracken, 1970). In contrast, a more recent tagging study by Zwanenburg[4] found that there was no evidence for seasonal migrations of haddock tagged on offshore banks in Division 4TVW, with the results indicating that these fish are relatively sedentary.

Similarly, resident stocks of haddock are found year round which do not appear to participate in such seasonal migrations (Schroeder, 1942; Halliday and McCracken, 1970). A relatively nonmigratory stock appears to remain localized around the Great South Channel–Nantucket Shoals region (Grosslein, 1962), although some of the stock may participate in seasonal migrations to the Bay of Fundy and Georges Bank (Schroeder, 1942). Likewise, when a large proportion of the stock along the western coast of Nova Scotia migrates to neighboring offshore banks, a resident inshore stock appears to remain there throughout the winter (Halliday and McCracken, 1970).

Results from the different tagging studies have shown that major stock divisions occur between haddock from New England and Nova Scotian waters.

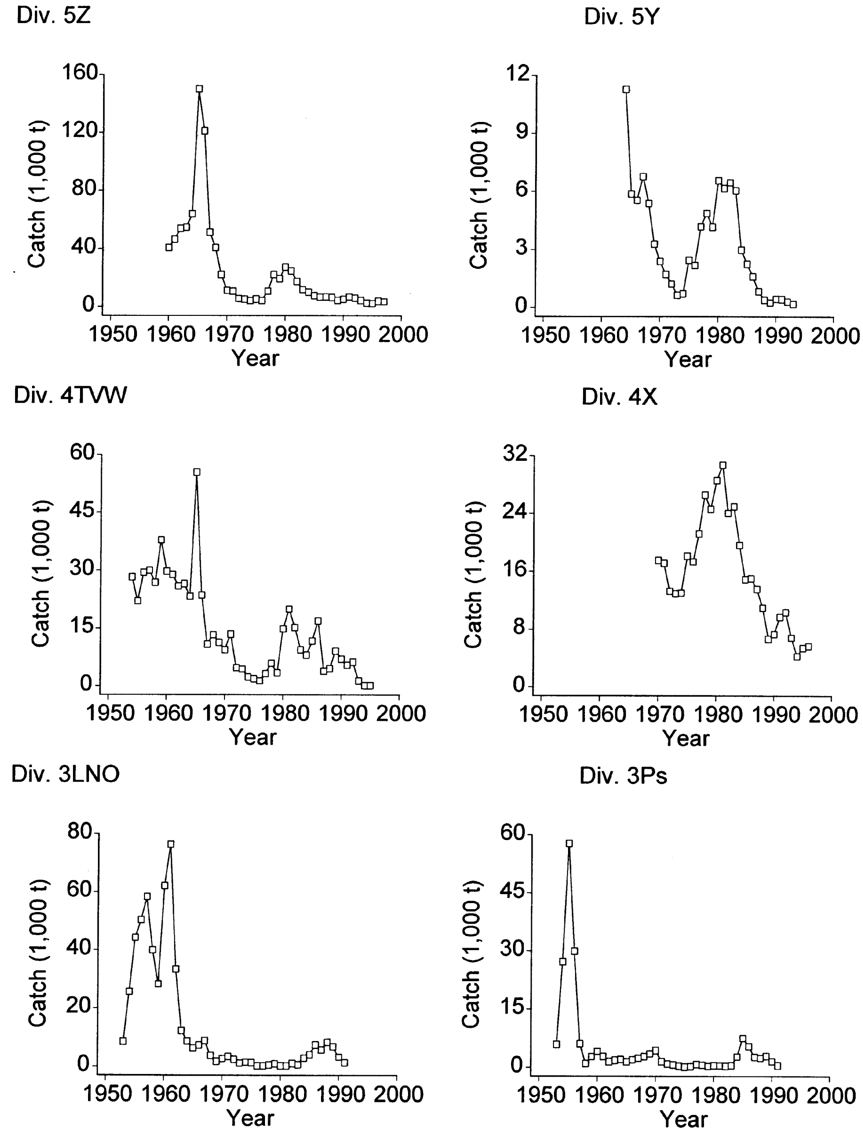

Figure 3.—Historical commercial catches (1,000 t) by stock division (Murphy and Bishop, 1995; Frank et al., 1997; Hurley et al., 1997; Brown, text footnote 1).

But how much interchange there is between haddock stocks from bank to bank or between inshore and offshore fishing grounds has not been answered by the various studies (Schroeder, 1942), although they have indicated that stock division probably does occur within each of the major regions. Also, it is difficult to discern from the tagging studies how much of the movements are seasonal migrations of more or less distinct stocks, and how much interchange there is between these stocks (Needler, 1930). Tagging of haddock has generally occurred throughout spring and summer and has been restricted to inshore waters, with very few fish tagged offshore, except for the more recent study by Zwanenburg.[4] Consequently, the patterns proposed by the earlier researchers may have been the results of examining a limited data set which described the movements of then extant inshore stocks of haddock (Zwanenburg[5]). Movement patterns

[4] Zwanenburg, K. C. T. 1987. Marine Fish Division, Bedford Institute of Oceanography, P. O. Box 1006, Dartmouth, N.S., Can., B2Y 4A2. Unpubl. data on file at the Bedford Institute of Oceanography.

[5] Zwanenburg, K. C. T. 1998. Marine Fish Division, Bedford Institute of Oceanography, P. O. Box 1006, Dartmouth, N.S., Can., B2Y 4A2. Personal commun.

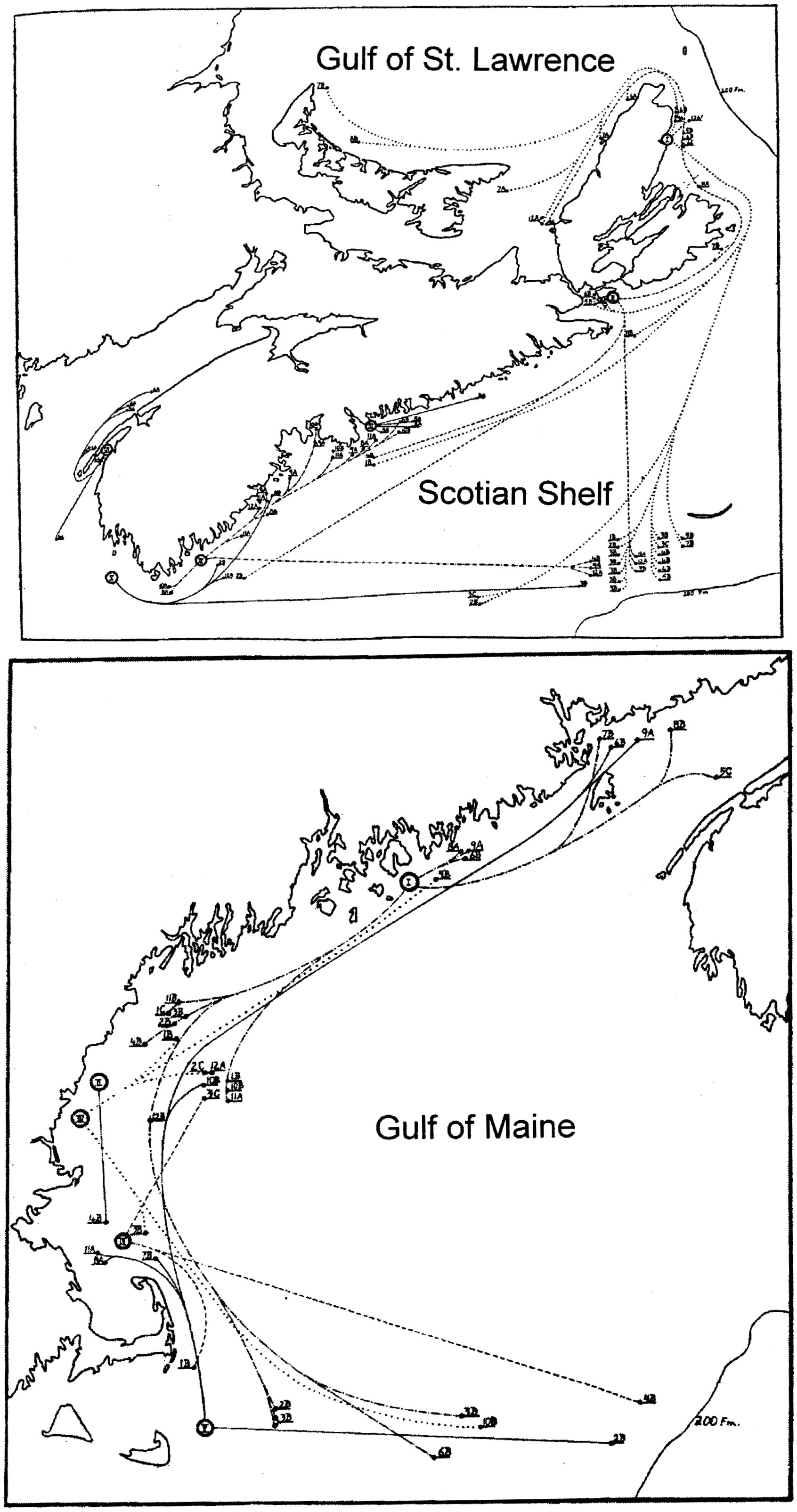

Figure 4.—Migration patterns of tagged haddock in New England and Nova Scotian waters showing little exchange between tagged fish in the two regions (Needler, 1930).

presented by the recaptures, therefore, is incomplete and may be biased by variable fishing effort. Also, the present patterns of distribution and movement may be difficult to compare to previous work in that the earlier population levels are so different from present very low levels (Zwanenburg[5]).

Demographics

Demographic or biological population parameters have been used to differentiate a finer scale of haddock stock separation in northwest Atlantic waters than that achieved by tag-recapture practices (Table 1). Growth differences of haddock from New England and Nova Scotian waters support the current stock units throughout these regions (Fig. 7). Needler (1930) observed differences in growth rates of haddock from corresponding inshore and offshore areas of New England and Nova Scotia, providing further evidence to the tag-recapture data of stock division between fish from these regions. Inshore Gulf of Maine (Div. 5Y) and offshore Georges Bank (Div. 5Z) haddock grew faster than those in coastal Nova Scotian waters and Browns Bank, respectively (Div. 4X). Likewise, Schuck and Arnold (1951) found significant differences in mean length-at-age between haddock from Georges Bank and Browns Bank, suggesting that little mixing occurs between fish from these regions.

As suggested by the tagging studies, stock structure was also apparent within each of the major regions, with the possibility of distinct inshore and offshore stocks. Haddock along the coast of the Gulf of Maine appear to grow slower than those fish from Nantucket Shoals and Georges Bank, indicating possible stock division between fish from these areas (Clark et al., 1982; Begg et al.[6]). Differential growth rates between haddock from the eastern part of Georges Bank and Nantucket Shoals suggested that fish from these areas may also be distinct stocks (Begg et al.[6]). Similarly, faster growth rates of inshore haddock than those from offshore waters of the

[6] Begg, G. A., J. A. Hare, and D. D. Sheehan. The role of life history parameters as indicators of stock structure. Manuscr. in review.

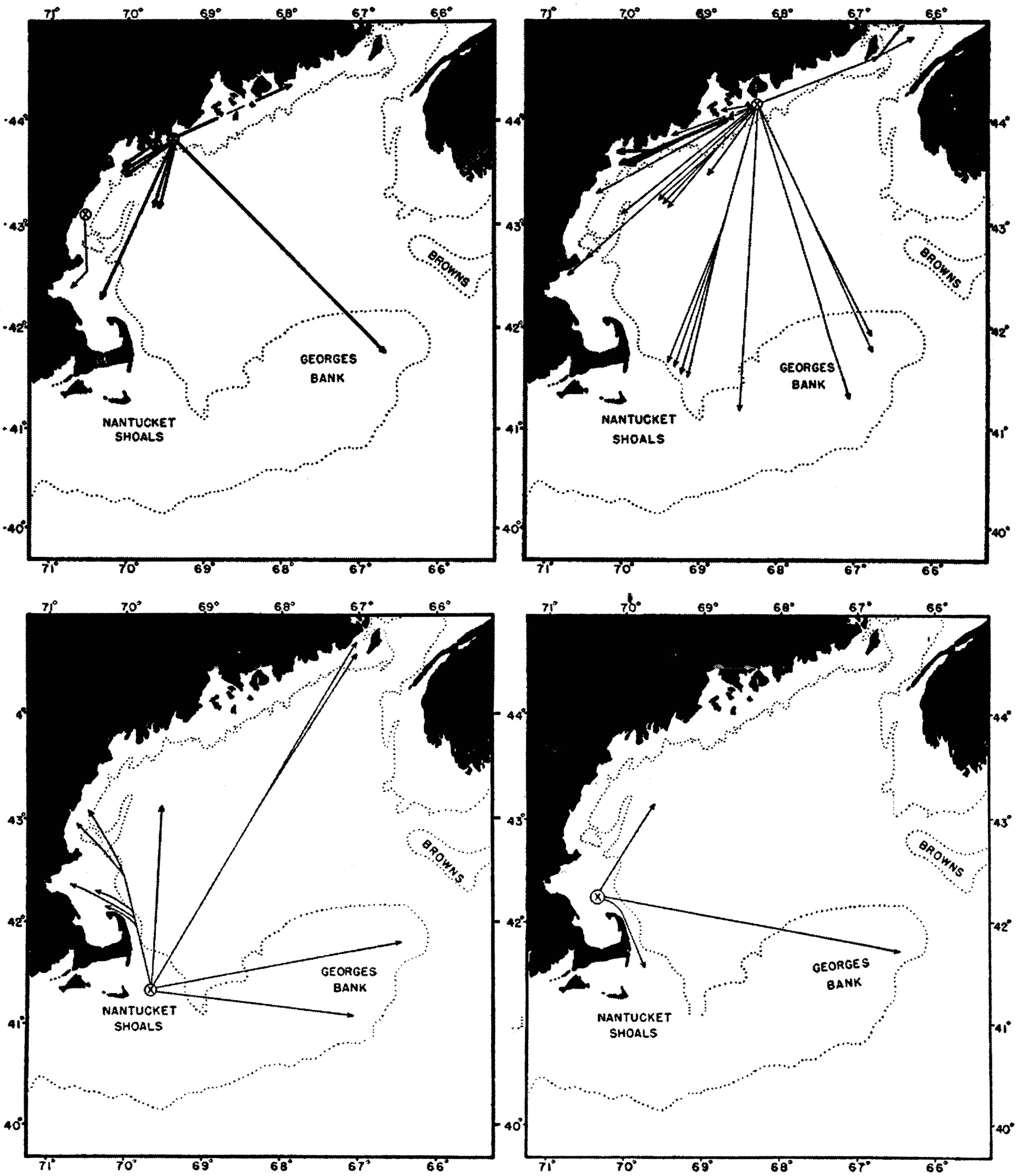

Figure 5.—Migration patterns of tagged haddock in New England waters, showing little exchange with Nova Scotian stocks, except in the Bay of Fundy (Schroeder, 1942).

Scotian Shelf suggested stock division within this region (Needler, 1930). Hennemuth et al. (1964) observed similar growth rates and age composition of haddock from the western (Div. 4X) and eastern (Div. 4VW) part of the Scotian

Shelf and the southern Gulf of St. Lawrence (Div. 4T). In contrast, haddock in the Bay of Fundy (Div. 4Xs) had a faster growth rate and younger age composition than those from waters off western Nova Scotia (Hennemuth et al., 1964), although these differences may have been influenced by gear selectivity problems and mixing of haddock from New England and Nova Scotian stocks within the bay. Beacham (1983) and Trippel et al. (1997) found differences in median lengths at sexual maturity among haddock from eastern and western Scotian Shelf waters, although these results were not statistically compared (Table 1). Haddock from the western Scotian Shelf (Div. 4X) tend to be larger and older at maturation than those from Georges Bank (Div. 5Z) (Overholtz, 1987), but smaller than those from St. Pierre Bank (Div. 3Ps) (Table 1). Stock separation of haddock within Newfoundland waters has been based mainly on differences in growth rates (Templeman et al., 1978a). Haddock on St. Pierre Bank typically grow faster and are of a greater mean length-at-age and length at first-maturity than those on the Grand Bank (Div. 3LNO) (Table 1) (Templeman et al., 1978a,b; Templeman and Bishop, 1979a,b).

Stock division of haddock inferred from several demographic characteristics has tended to agree with patterns developed from the tag-recapture studies. However, for the most part, individual regional growth curves have not been compared in a statistically rigorous fashion to determine the significance, if any, of the apparent growth differences used to separate the stocks (Schuck and Arnold, 1951). Needler (1930) only presented average length-at-age data, and samples were taken by commercial fishing gear which excluded younger haddock, while probably selecting for larger sizes of specific aged fish. Consequently, discrepancies in growth rates estimated by Needler (1930) and Hennemuth et al. (1964) may have been related to differences in sampling and analytical methodologies. Differences in sampling times and gear types between the various studies has resulted in a lack of homogeneity in the origin of the samples used to provide demographic characters to differentiate haddock stocks. Also,

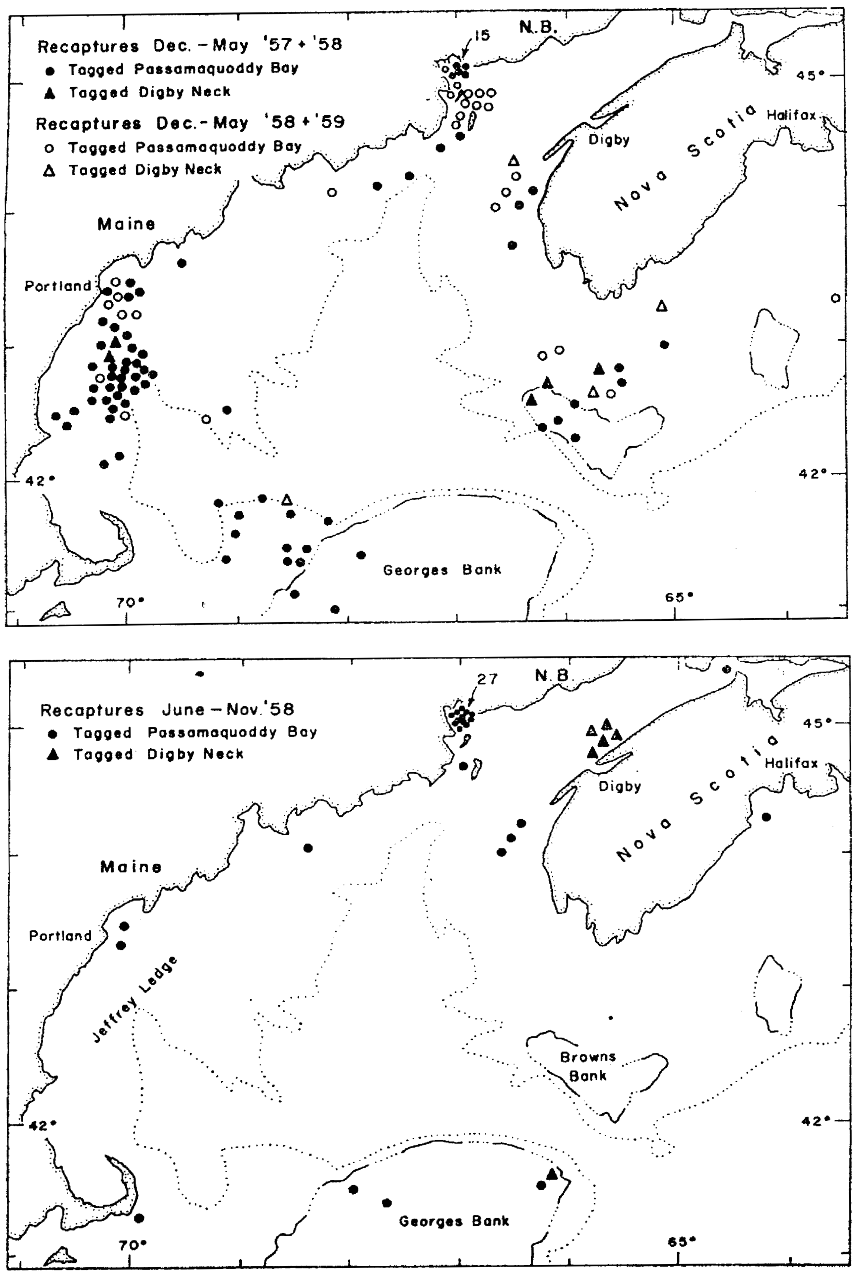

Figure 6.—Seasonal migrations of haddock in New England and Nova Scotian waters, tagged along the eastern and western shores of the Bay of Fundy (McCracken, 1960).

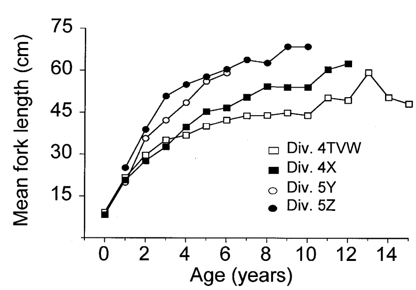

Figure 7.—Growth differences in mean lengths at age among haddock stocks Div. 4TVW (Frank et al., 1997), 4X (Hurley et al., 1997), 5Y and 5Z (calculated from 1997 NMFS Northeast Fisheries Science Center spring bottom-trawl survey data).

while the magnitude of the differences in growth rates that have been detected among haddock from some regions may be sufficiently large to indicate real differences in the stocks (Hennemuth et al., 1964), these differences may be the result of demographic plasticity within stocks as a response to changing ambient abiotic and biotic conditions.

Spawning and Recruitment Patterns

Spawning Times and Locations

Further evidence for stock discrimination of haddock within New England and Nova Scotian waters has been provided by spawning and recruitment patterns of the species in relation to the distinct oceanographic conditions of each region. Peak spawning of haddock occurs in late March and early April within New England (Marak and Livingstone, 1970; Grosslein and Hennemuth, 1973; Lough and Bolz, 1989), from late April to June in Nova Scotia (Hurley and Campana, 1989; Page and Frank, 1989; Waiwood and Buzeta, 1989), and throughout June and July in Newfoundland waters (Templeman et al., 1978b; Templeman and Bishop, 1979b). Spawning periodicity of haddock is highly variable and appears to be correlated with water temperature, resulting in delayed spawning during colder years and advanced spawning during warmer years (Page and Frank, 1989).

Throughout the northwest Atlantic the main spawning grounds of haddock occur over Georges Bank (Div. 5Z), the western part of the Scotian Shelf (Div. 4X), Gulf of Maine (Div. 5Y), Nantucket Shoals (Div. 5Z), Emerald-Western Banks (Div. 4VW), Grand Bank (Div. 3LNO), and St. Pierre Bank (Div. 3Ps) (Fig. 8) (Colton and Temple, 1961; Smith and Morse, 1985; Page and Frank, 1989). Along the Scotian Shelf the primary spawning grounds occur on Browns Bank (Div. 4X) and Emerald-Western Banks (Div. 4VW), with lower levels on adjacent banks and in inshore coastal areas (Hurley and Campana, 1989; Campana et al., 1989). Buoyancy characteristics of haddock eggs and local physical and oceanographic conditions may result in hatching failure throughout these inshore waters (Frank

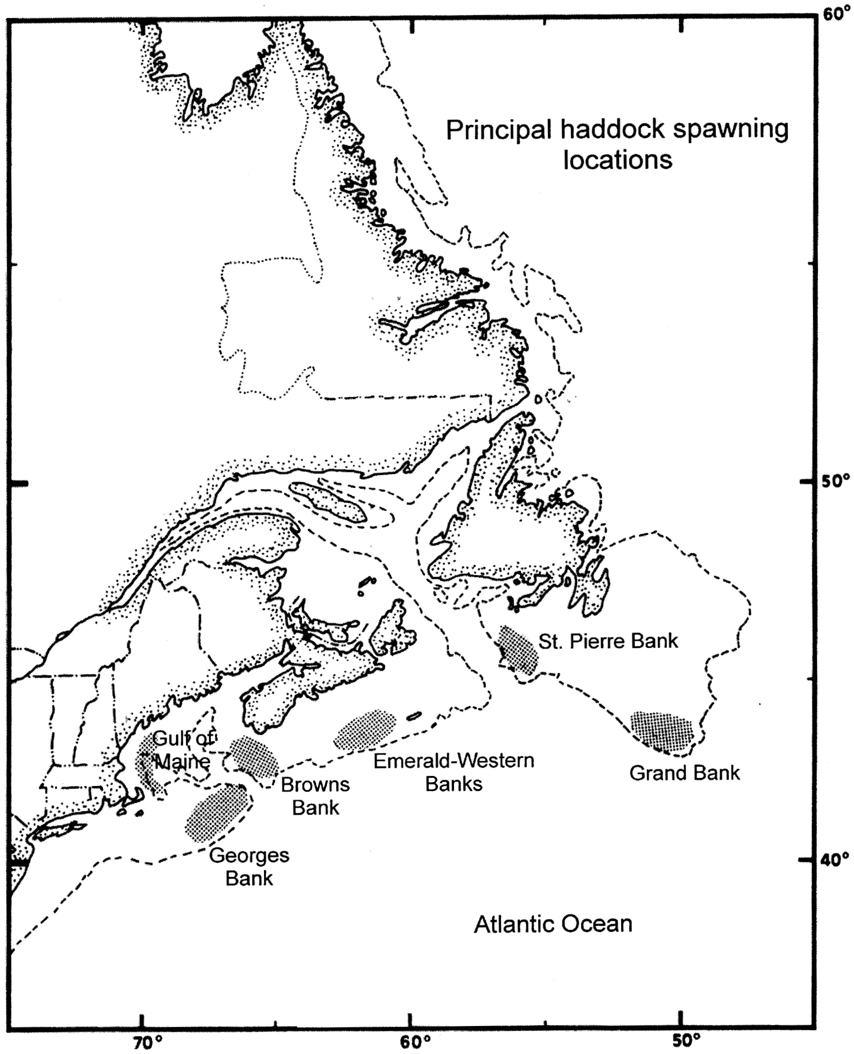

Figure 8.—Principal spawning locations of haddock in the northwest Atlantic (Page and Frank, 1989).

Table 1.—Summary of biological parameters (length/age at 50% maturity: L_{50}, A_{50}; and von Bertalanffy growth coefficients: L_∞, K, t_0) derived for each haddock stock Div. 3LNO, 3Ps, 4TVW, 4X, 5Y, and 5Z.

	Stock division					
Parameter	3LNO	3Ps	4TVW	4X	5Y	5Z
L_{50} (cm) females	51[1]	50[3]	30[4]	38[4]	39[7]	39[7]
L_{50} (cm) males	44[1]	40[3]	29[4]	33[4]	27[7]	31[7]
A_{50} (years) females	5.1[1]	4.3[3]	3.4[4]	3.6[4]	2.8[7]	2.4[7]
A_{50} (years) males	4.0[1]	3.3[3]	2.9[4]	3.3[4]	1.9[7]	1.8[7]
L_∞	74.8[2]	84.6[2]	51.3[5]	76.6[6]	72.9[8]	73.8[8]
K	0.10[2]	0.24[2]	0.26[5]	1.12[6]	0.35[8]	0.38[8]
t_0	–3.6[2]	0.47[2]	–0.97[5]	0.18[6]	0.30[8]	0.17[8]

[1] Templeman et al. (1978b).
[2] Templeman and Bishop (1979a).
[3] Templeman and Bishop (1979b).
[4] Trippel et al. (1997).
[5] Calculated from mean lengths-at-age reported in Frank et al. (1997).
[6] O'Boyle et al. (1988).
[7] Begg et al., text footnote 6.
[8] O'Brien et al. (1993).

et al., 1989). Significant spawning also occurs on the southwestern portion of Banquereau Bank, but this appears to occur only during high population density and as such may represent spillover from the Emerald-Western spawning grounds (Zwanenburg[5]). Spawning of haddock occurs near the substratum during spring when the water column is beginning to stratify, resulting in the eggs floating to the surface (Walford, 1938). Although eggs in early stages of development are concentrated in the surface layers, the proportion in deeper waters increases as eggs develop, thereby reducing the effects of wind-driven transport in dispersal from the spawning grounds (Page et al., 1989).

Retention of Spawning Products

Surface circulation patterns within New England waters are dominated by seasonally variable gyres that are counterclockwise in the Gulf of Maine and clockwise on Georges Bank (Fig. 9) (O'Boyle et al., 1984; Loder et al., 1988; Drinkwater, 1996). These patterns tend to retain eggs and larvae in the areas from which they originate. Larvae originating on Georges Bank are transported in a westerly direction, but are mostly retained on the bank that acts as both a spawning and nursery area (Grosslein and Hennemuth, 1973; Sherman et al., 1984; Smith and Morse, 1985; Lough and Bolz, 1989). Larvae that are spawned on the northeast section of Georges Bank during spring have a continuous recruitment to the central part of the bank as they develop and are advected there along its southern flank (Lough and Bolz, 1989). However, transport of larvae off Georges Bank can occur due to unusually strong geostrophic currents, such as in the spring of 1987, with sufficient magnitude to be an important factor influencing the stock composition of neighboring southwesterly regions, such as Nantucket Shoals (Polacheck et al., 1992). Most of the larvae associated with the outside of the Georges Bank gyre pass south of the Great South Channel, where no evidence of significant spawning has been detected, and settle throughout the Nantucket Shoals region (Smith and Morse, 1985).

Likewise, on the Scotian Shelf distributions of haddock larvae are associated with gyres that tend to concentrate and maintain spawning products over relatively shallow banks of the shelf, thereby playing a functional role in maintenance of stock integrity (Fig. 10) (O'Boyle et al., 1984; Smith, 1989). Campana et al. (1989) proposed that drift and retention processes operate together on the permanent, tidally induced, clockwise gyre around Browns

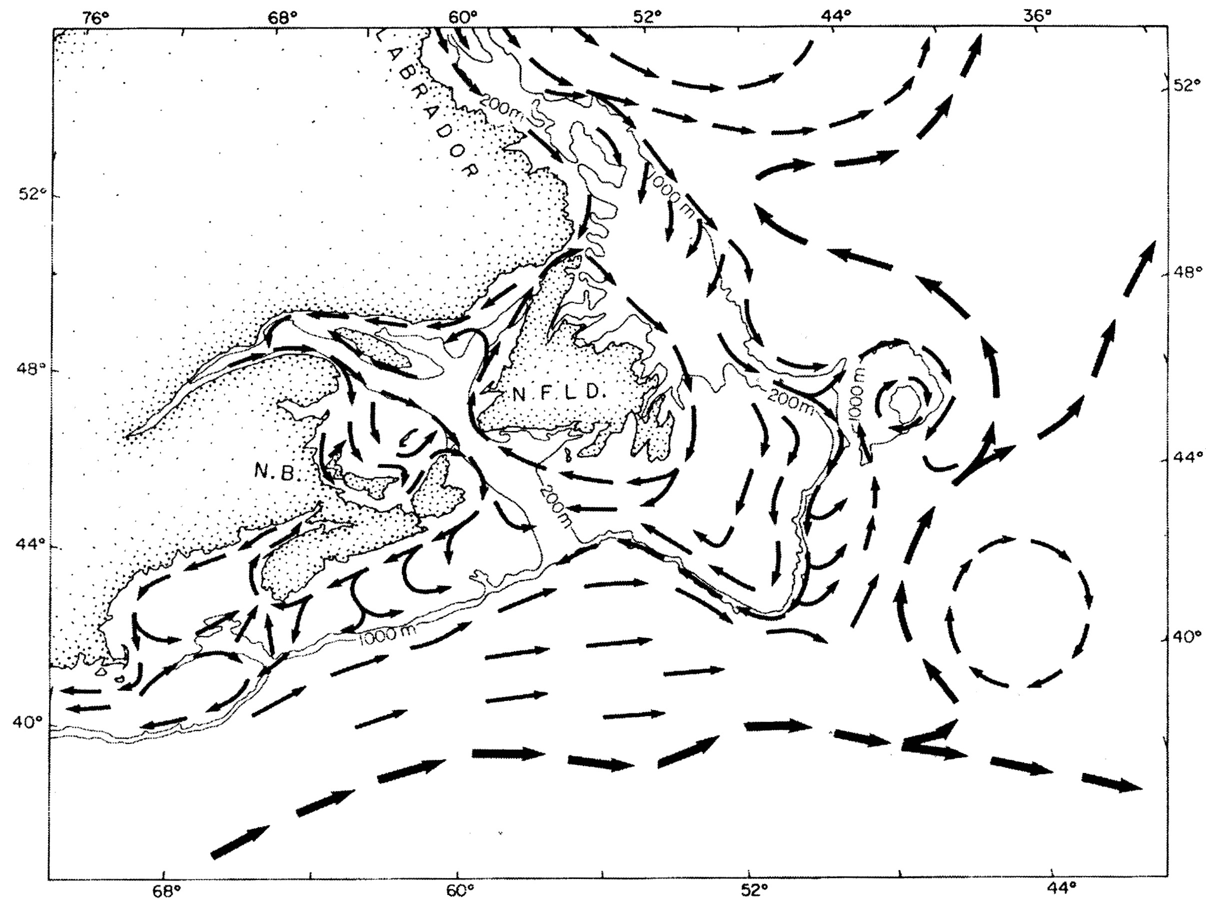

Figure 9.—General circulation patterns within the northwest Atlantic Ocean (O'Boyle et al., 1984).

Bank to retain some larvae on the bank, while transporting others towards inshore waters and to the Bay of Fundy, creating a single retention zone or unit stock throughout this region (Div. 4X). Although larvae are retained on the western banks of Nova Scotia, the same does not appear to occur on most of the eastern banks, which may be explained by the existence of gyres in the former areas acting as larval entrainment mechanisms (O'Boyle et al., 1984). Frank (1992) proposed a density-dependent dispersive model for haddock stocks in these waters, where he suggested juvenile haddock of strong year classes disperse from their spawning grounds in Division 4VW to those in Division 4X, thereby supplementing and assisting in the stability of the stock in Division 4X.

Smith and Morse (1985) found that haddock eggs and larvae originating on Georges Bank, Gulf of Maine, and Scotian Shelf spawning grounds do not intermix, and hence, are geographically isolated and constitute separate stocks. On Georges Bank, two spawning aggregations appear to exist with one on the Northeast Peak ("Eastern Georges Bank") and the other around Nantucket Shoals ("Western Georges Bank") (Fig. 11). The depth and strong currents associated with the Fundian Channel provides a natural boundary for separating spawning products from Georges Bank and the Scotian Shelf spawning grounds. Likewise, the broad, deep central basin of the Gulf of Maine may isolate eggs and larvae on the Scotian Shelf from those in coastal New England waters (Smith and Morse, 1985). Little evidence of ichthyoplankton exchange between Georges and Browns Banks supports the hypothesis of isolation and maintenance of distinct stocks of haddock within these regions (Hurley and Campana, 1989). Similarly, data from the NMFS Northeast Fisheries Science Center spring bottom-trawl surveys, 1988–97, indicate a relatively discontinuous distribution of haddock spawning aggregations (Georges Bank, Nantucket Shoals, Gulf of Maine, Browns Bank, and along the inshore western Scotian Shelf) (Fig. 11).

Synchrony of Recruitment

Interrelationships may exist between haddock stocks throughout the Gulf of Maine, Georges Bank, Nantucket Shoals, and Browns Bank, as the same year classes have historically tended to show similar patterns in recruitment throughout this entire region (Clark et al., 1982; Koslow, 1984; Koslow et al., 1987; Thompson and Page, 1989). Recent studies have suggested large-scale physical and biological forcing are partly responsible for synchrony in recruitment and year-class success among different stocks (Koslow, 1984; Koslow et al., 1987). However, Cohen et al. (1991) indicated local-scale processes, rather than large-scale physical forcing, dominate recruitment patterns, because

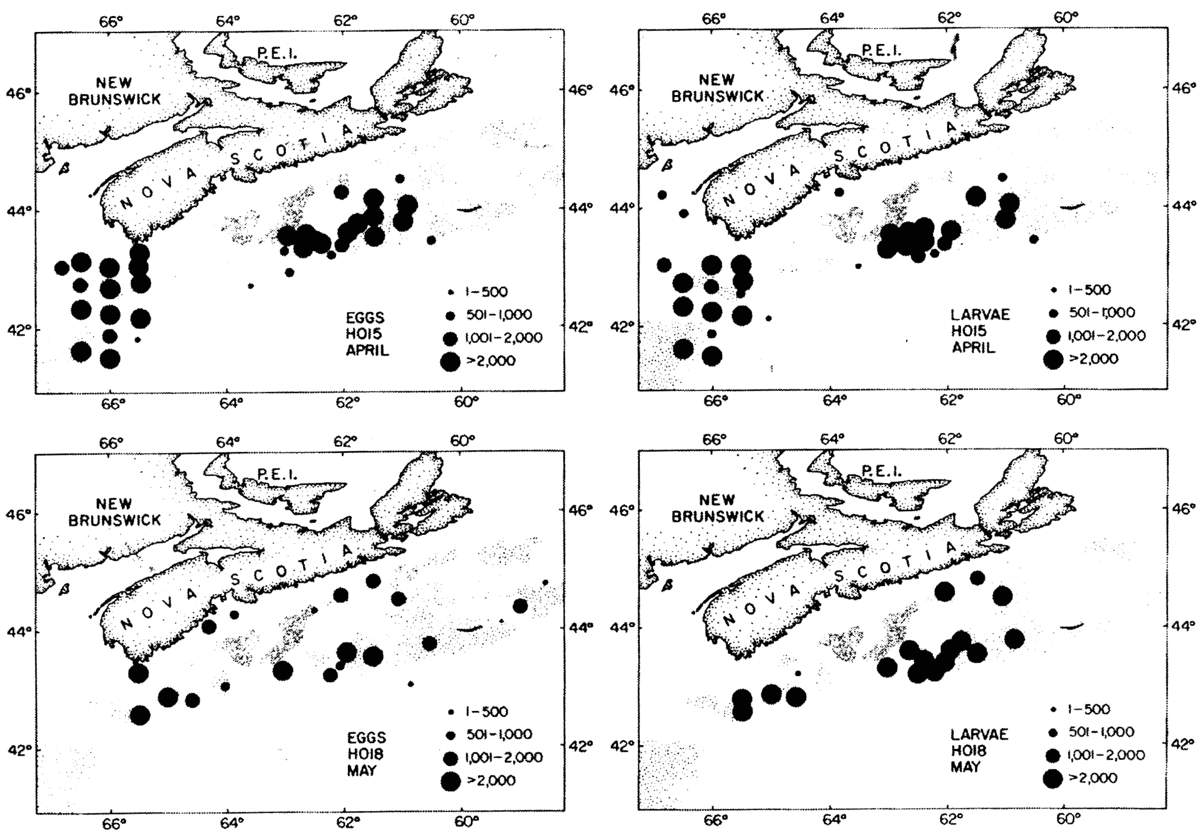

Figure 10.—Spatial and temporal distributions of haddock eggs and larvae on the Scotian Shelf (O'Boyle et al., 1984).

most significant correlations were found between neighboring stocks.

Meristics and Morphometrics

Meristic characters, in the form of vertebral number, have been used to provide insights into stock structure of haddock (Clark and Vladykov, 1960; Tremblay et al., 1984; Vladykov[7]). Vladykov[7] used vertebral counts of adult haddock to confirm the three population groups suggested by Needler (1930): New England, Nova Scotia, and Newfoundland. After updating this meristic analysis, Clark and Vladykov (1960) proposed that the Nova Scotia stock be divided into three stocks: eastern, central, and western Nova Scotia. Mean number of vertebrae differed significantly between the five stocks and increased with latitude from New England to the eastern Scotian Shelf, suggesting an inverse relationship with water temperature (Fig. 12). In contrast, Tremblay et al. (1984) found lower vertebral numbers for juvenile haddock from the northeastern part of the Scotian Shelf (Div. 4V) than those from central (Div. 4W) and western Nova Scotian waters (Div 4X). Based on these differences, they proposed that the haddock stock occupying the northeastern and central area (Div. 4VW) of the Scotian Shelf be divided into two stock components: eastern Scotian Shelf (Div. 4V) and central Scotian Shelf (Div. 4W).

A major limitation of these meristic studies has been the lack of temporal comparisons to examine the consistency of stock structure patterns over time. Spatial comparisons have also been restricted, with few inshore samples having been collected. Results presented by Tremblay et al. (1984) were mean values and were not accompanied by data showing the amount of variability both within and between samples. Consequently, it is difficult to comment on the validity of the differences in their results compared to those of Clark and Vladykov (1960). The actual degree of mixing between stocks cannot be estimated from any of the meristic studies, and the minor differences used to separate stocks should be viewed with caution, particularly given the high degree of environmentally influenced plasticity that can exist in meristic characters.

More recently, otolith shape analysis was investigated to determine its utility as a tool for stock discrimination of haddock stocks in the northwest Atlantic (Begg[8]). Several shape variables

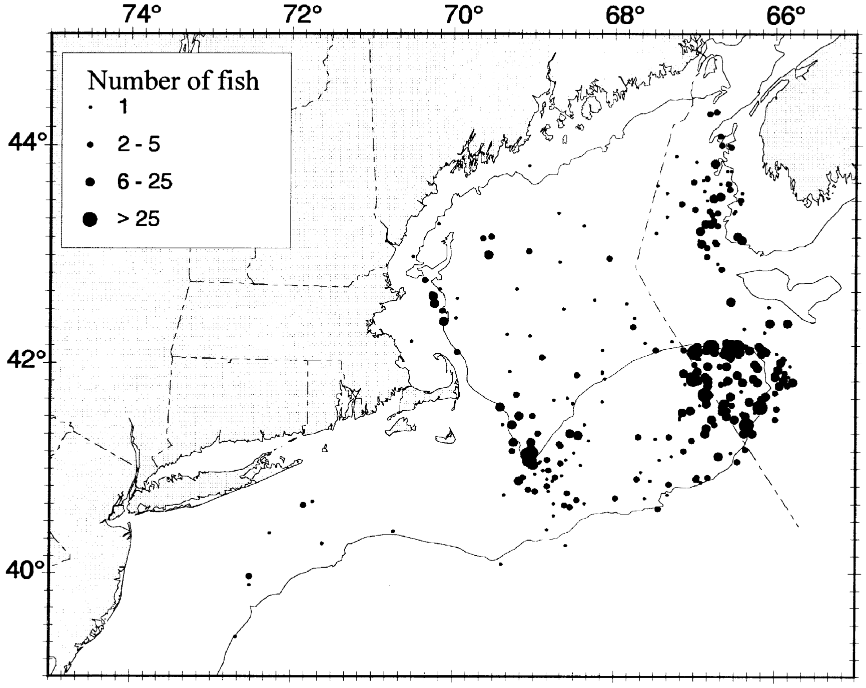

Figure 11.—NMFS Northeast Fisheries Science Center spring bottom-trawl survey catch (number) per tow of sexually mature haddock, 1988–97.

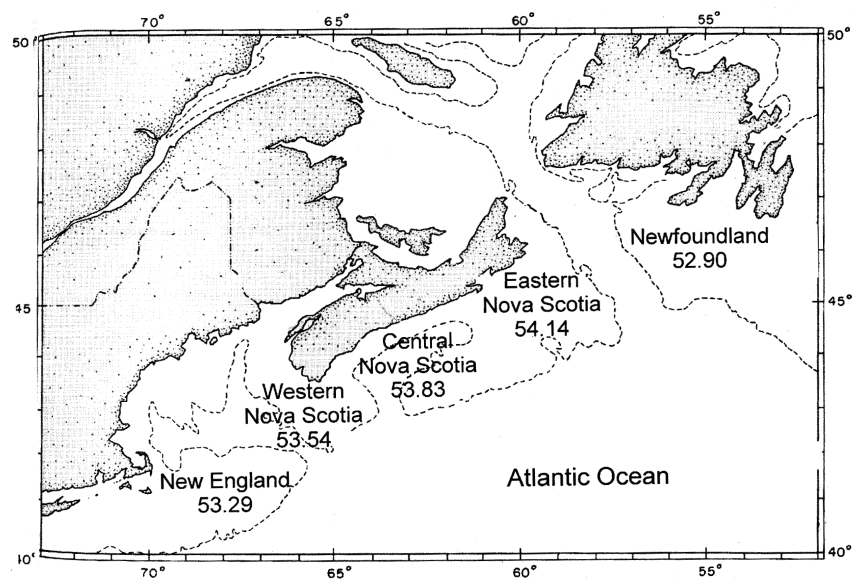

Figure 12.—Mean vertebrae number of haddock from fishing grounds of the northwest Atlantic Ocean (Clark and Vladykov, 1960).

[7] Vladykov, V. D. 1935. Haddock races along the North American coast. Biol. Board Can., Atl. Prog. Rep. 14:3-7.

[8] Begg, G. A. 1998. Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, 166 Water Street, Woods Hole, MA 02543. Unpublished data on file at the Northeast Fisheries Science Center.

were statistically significant between haddock samples from Georges Bank, the Gulf of Maine, and the Scotian Shelf, providing a phenotypic measure of stock separation.

Parasites

The use of parasites for stock identification of haddock in the northwest Atlantic has been limited to a preliminary study by Scott (1981). A total of 19 species of alimentary-tract parasites of haddock from the Scotian Shelf were identified, although most of them were ubiquitous, occurring in a variety of hosts over wide geographical areas. Only two species (Digenea: *Lepidapedon rachion* and Myxosporida: *Myxidium bergense*) showed the degree of host specificity, abundance, and correlation with known haddock stock delineation needed to be considered prospects for biological tags. Infestation of *L. rachion* in haddock from Browns Bank (Div. 4X) was higher than those from the Bay of Fundy (Div. 4Xs) and lower than those from the Emerald-Banquereau area (Div. 4W), providing indirect evidence for separate stocks in these areas (Scott, 1981). Of interest is that parasites have been used successfully to distinguish haddock stocks in the northeast Atlantic. Lubieniecki (1977) analyzed the incidence and intensity of infestation with *Grillotia erinaceus* plerocerci to indicate a number of separate stocks of haddock within this region. In contrast, Scott (1981) found that *G. erinaceus* was not a major parasite in haddock from the northwest Atlantic, thereby reducing its utility as a biological tag in these waters.

Genetics

Genetic information obtained from mitochondrial DNA procedures has not been considered in construction of the present management units of haddock stock structure in the northwest Atlantic (Zwanenburg et al., 1992), although genetically discrete stocks have been identified using electrophoretic techniques in northeastern Atlantic waters (Jamieson and Birley, 1988). Importantly, the stock structure of haddock identified by the genetic results of Jamieson and Birley (1988) was consistent with the parasitic study of Lubieniecki (1977).

Examination of mitochondrial DNA in haddock from the northwest Atlantic has provided conflicting information on the stock structure of the species in this region. Zwanenburg et al. (1992) determined that haddock sampled from offshore banks of New England (Georges, Div. 5Z), Nova Scotia (Browns, Div. 4X; Western, Div. 4W; Banquereau, Div. 4V), and Newfoundland (St. Pierre, Div. 3Ps) were comprised of a mixture of divergent genotypes that may have arisen in past populations that were more isolated than those at present. Although, no statistically significant differences in pair-wise comparisons of genotype frequencies among haddock from any of the banks were detected, gene flow among the population was considered to be restricted. A geographic cline in genotype frequency, increasing genetic differences with geographic distance (Fig. 13), and the deep ocean channels acting as barriers to gene flow formed the basis for their reasoning of stock separation. In contrast, Purcell et al. (1996) suggested that haddock on Georges Bank may not comprise a genetically discrete stock. They hypothesized that significant heterogeneity in haplotype frequencies observed in haddock samples from the 1975 and 1985 cohorts from Georges Bank was caused by episodic intrusions of Scotian Shelf surface water onto the bank resulting in larvae from different regions contributing to the gene pool of haddock in this area. However, Purcell et al. (1996) also recognized that heterogeneity in mtDNA markers may have been due to mixing of the spawning aggregations on the Northeast Peak and Nantucket Shoals.

Table 2.—Results of stock identification studies to differentiate haddock stocks in the Northwest Atlantic.[1]

	Stock structure (no. of stocks identified within)		
Stock I.D. method	New England	Nova Scotia	Newfoundland
Tag-recapture	1-2 (5Y; 5Z / N.Sh.?)	2 (4X; 4TVW)	N/A
Growth rates	2-3 (5Y; 5Z; N.Sh.?)	2 (4X; 4TVW)	2 (3Ps; 3LNO)
Spawning patterns	2-3 (5Y; 5Z; N.Sh.?)	2 (4X; 4TVW)	2 (3Ps; 3LNO)
Meristics	N/A	3-4 (4X; 4V; 4W; 4T?)	N/A
Parasites	N/A	3 (4Xs; 4X; 4W)	N/A
Genetics	?	?	N/A
Current management units	1(Canada) / 2 (USA) (5Zjm - Canada; 5Z, 5Y-USA)	2 (4X; 4TVW)	2 (3Ps; 3LNO)

[1] Key: Div. 5Zjm - Georges Bank, Canada; Div. 5Z - Georges Bank, USA; Div. 5Y - Gulf of Maine; N.Sh. - Nantucket Shoals; Div. 4X - Western Nova Scotia; Div. 4Xs - Bay of Fundy; Div. 4W - Central Nova Scotia; Div. 4V - Eastern Nova Scotia; Div. 4T - Gulf of St. Lawrence; Div. 3Ps - St. Pierre Bank; Div. 3LNO - Grand Bank. N/A = No data available. ? = Results uncertain.

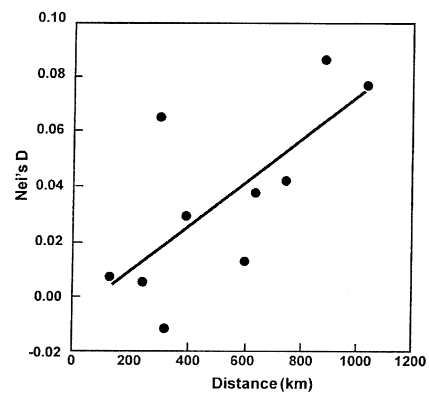

Figure 13.—Relationship between genetic difference (Nei's *D*) and geographic distance separating haddock on northwest Atlantic banks (Zwanenburg et al., 1992).

Discussion

Current management units for haddock in the northwest Atlantic tend to encompass discrete populations identified on a biological stock basis, although further investigation into the stock structure of haddock in New England and Nova Scotian waters is required (Table 2). Correspondence of the species' biological stock structure with that of its current management units was largely the result of the overriding importance of haddock and Atlantic cod, *Gadus morhua*, to the fishery when the stock boundaries in the northwest Atlantic were originally identified in 1932 by the North American Council on Fishery Investigations, and in 1951 by the International Commission for the Northwest Atlantic Fisheries, as information on stock separation was only available for these two species at those times (Halliday and Pinhorn, 1990).

Stock Structure

Throughout the northwest Atlantic, haddock stock structure is divided into three components (New England, Nova Scotia, Newfoundland) by the Fundian and Laurentian Channels that act as barriers to dispersal (Needler, 1930). Within each of these major population divisions, a number of separate haddock stocks exist.

Tag-recapture data, growth rate information, and spawning and circulation patterns within New England waters indicate that there is a resident stock of haddock on Georges Bank (Div. 5Z) and a separate seasonally migrating stock along the coast of the Gulf of Maine (Div. 5Y) (Needler, 1930; Schroeder, 1942; Grosslein, 1962; Smith and Morse, 1985). Growth and spawning data suggest that a discrete stock may also be present in the Nantucket Shoals region (Needler, 1930; Smith and Morse, 1985), although haddock from this area may be a mixture of fish from the Gulf of Maine and Georges Bank. Separation of these stocks may be enhanced by the Great South Channel, although it probably does not have the same effect on dispersal as the other much deeper channels in the northwest Atlantic. A considerable degree of uncertainty still remains in the current views of haddock stock structure within New England waters, particularly over the discreteness of the Nantucket Shoals population and, to a lesser extent, that in the Gulf of Maine.

A range of stock identification techniques suggests a complex stock structure is evident for haddock along the Scotian Shelf, although there is disagreement over the amount of separation (Table 2). At least two major stock divisions occur in Nova Scotian waters, comprising haddock from an eastern (Div. 4TVW) and western Scotian Shelf stock (Div. 4X) (Martin, 1953; Grosslein, 1962; Bowen, 1987). These stocks appear to be relatively distinct with limited mixing between them except along the coast during summer when haddock from inshore waters of the western stock move eastward, and in winter when those from the eastern stock move southwest (McCracken[3]). However, Frank (1992) found that the spatial dynamics of haddock year classes on the Scotian Shelf are consistent with a pattern of unidirectional mixing of stocks during the pelagic juvenile stage, then a mixed-stock composition up to the age of maturation, followed by a return migration of adult fish to their natal sites. Consequently, Frank (1992) suggested that the management unit on the Scotian Shelf should include both Division 4X and Division 4VW stocks until the potential flux across these stock boundaries is resolved.

Haddock from the eastern Scotian Shelf stock appear to be closely related to those in the southern Gulf of St. Lawrence, and probably belong to the same stock (Halliday, 1971), although comparative data for these regions are limited. Lack of biological data for stock discrimination from the eastern Scotian Shelf and the southern Gulf of St. Lawrence precludes confirmation of these purported stock units. Few haddock have been tagged in these waters to determine movement patterns, and samples required for demographic and spawning patterns have been limited. Uncertainty exists over the stock status of inshore haddock from the southern Scotian Shelf and Bay of Fundy stock (Div. 4X); however, haddock in the latter area may be a mixture from the Gulf of Maine and western Scotian Shelf stocks.

Although little tagging data exist for haddock in Newfoundland waters, eastern Scotian Shelf waters, and the southern Gulf of St. Lawrence, it is reasonable to assume that there is little interchange between haddock from these areas and those to the southwest, as the Laurentian Channel is probably an even more effective barrier than the Fundian Channel since it is considerably wider and deeper (Needler, 1930). Within Newfoundland waters, two main haddock stocks exist, one on Grand Bank (Div. 3LNO) and the other on St. Pierre Bank (Div. 3Ps) (Table 2). Haddock from these two areas are thought to not mix extensively and are considered to be separate stocks based on persistent differences in growth rates and year class compositions (Templeman, 1953; Grosslein, 1962; Templeman and Bishop, 1979a; Halliday and Pinhorn, 1990).

Stock Identification Techniques

Combined information from tag-recapture, demographic, spawning, recruitment, meristic, parasitic, and genetic studies have provided evidence for the identification of haddock stocks throughout the northwest Atlantic (Table 2). Tag-recapture data identified a broad-scale pattern of haddock stock structure in the northwest Atlantic, but provided no conclusive information on stock structure within each of the major regions (Needler, 1930; Schroeder, 1942; McCracken, 1960; Halliday and McCracken, 1970). Recapture data, however, first indicated that New England and Nova Scotian stocks may not be homogeneous units, but instead may be comprised of a number of separate stocks (Needler, 1930; Halliday and McCracken, 1970).

Growth differences between haddock from regions within the northwest Atlantic provided evidence in support of tagging results, which indicated that haddock may return to the same locality to spawn (Needler, 1930; Schuck and Arnold, 1951), resulting in stocks being reproductively isolated and demographic differences subsequently maintained. Zwanenburg et al. (1992) also suggested that haddock home with high fidelity to their natal banks to spawn, thereby maintaining stock separation. Consequently, the amount of mixing between different parts of the population of the different regions may not be sufficient to mask local stock differences (Needler, 1930).

Meristic studies agreed with the general stock structure of haddock proposed by Needler (1930), although they indicated that there may be three to four separate stocks within Nova Scotian waters (Clark and Vladykov, 1960; Tremblay et al., 1984; Vladykov[7]). In contrast, conflicting genetic results have not improved our understanding of haddock stock structure in the northwest Atlantic, because mtDNA procedures may not be sensitive enough to identify fine-scale population structure (Purcell et al., 1996). The incongruity between the studies of Zwanenburg et al. (1992) and Purcell et al. (1996) is probably partly responsible for the lack of consideration of genetics in the delineation and management of the species stocks. The utility of genetic-based methods in providing a clearer resolution of haddock stock structure will require considerably more samples (Purcell et al., 1996), both of a temporal and spatial component. In addition, a detailed understanding of the extent of both current and historical divergence of haddock stocks will enable assessment of historical changes in stock structure (Purcell et al., 1996).

The various techniques used to identify stock structure of haddock in the northwest Atlantic have tended to agree on the major stock divisions between New England, Nova Scotia, and Newfoundland waters, but they have differed partly in the degree of separation found within each of these regions (Table 2). These differences are probably related to the sensitivity of each method in detecting stock separation and the limitations associated with each technique. Tagging studies of haddock have generally been restricted to inshore waters in spring and summer, with few fish having been tagged on important offshore banks where major spawning aggregations occur (Needler, 1930; Schroeder, 1942; McCracken, 1960; Halliday and McCracken, 1970). Consequently, the degree of interchange between stocks from inshore and offshore fishing grounds and their relative discreteness cannot be determined from these studies. Typically, the demographic studies have only presented average length-at-age data, thereby precluding examination of the amount of variability in the data and the level of significance used to determine differences in stock dynamics (Needler, 1930). Gear selectivity problems, differences in sampling times, and the general lack of homogeneity in samples have also tended to confound the results of these studies (Schuck and Arnold, 1951; Hennemuth et al., 1964).

Spawning (Grosslein and Hennemuth, 1973; Sherman et al., 1984; Smith and Morse, 1985; Lough and Bolz, 1989), recruitment (Clark et al., 1982; Koslow, 1984; Koslow et al., 1987; Thompson and Page, 1989), meristic (Clark and Vladykov, 1960; Tremblay et al., 1984; Vladykov[7]), parasitic (Scott, 1981), and genetic (Zwanenburg et al., 1992; Purcell et al., 1996) stock identification studies of haddock have usually been restricted in their temporal and spatial comparisons, effectively preventing examination of the temporal persistency in stock structure patterns. Inadequate spatial samples, particularly from inshore waters, have made it difficult to determine the connectivity and relative separation of stocks found on inshore and offshore fishing grounds, a topic that requires considerably more investigation if a finer resolution of haddock stock structure in the northwest Atlantic is to be achieved.

Future Research

Stock identification is a necessary precursor for effective fisheries management (Kutkuhn, 1981). Although a number of haddock stocks in the northwest Atlantic have been identified using a combination of traditional techniques, uncertainty remains in the discreteness of stocks in New England and Canadian waters. This lack of understanding of haddock stock structure can limit the ability to develop and implement effective stock rebuilding programs throughout the region. Such knowledge is useful for setting management restrictions in fisheries which contain several stocks with different levels of exploitation, as less productive stocks may be seriously depleted or eliminated if exploited with fishing rates that adequately exploit more productive stocks in a mixed fishery (Ricker, 1958).

Future research examining the stock structure of haddock in these regions should advance existing studies by utilizing more recent, innovative stock identification techniques such as chemical analysis of calcified structures that have proved useful for differentiating among Atlantic cod stocks (Campana et al., 1994). Contemporary stock identification tools such as otolith marking and image analysis procedures should also be investigated to determine their utility for discrimination of haddock stocks in the northwest Atlantic. A combination of techniques should be used in unison to strengthen and confirm any suggested stock structure provided by a single procedure in isolation owing to the inadequacies associated with any particular method (i.e. an integrated holistic approach to stock identification) (Begg and Waldman[9]).

Population dynamic models used in fisheries management need to be developed that incorporate multistock complexes and demographic consequences of dispersal, such as the more recent metapopulation models (Frank, 1992). Such models may be particularly relevant for haddock stocks along the Scotian Shelf and in other regions of the northwest Atlantic that appear to migrate and mix with other stocks at certain times of the year. Although most fisheries are managed on a single-species basis, there is a general recognition that multispecies interactions are an important component of marine ecosystem dynamics which should be considered in contemporary management plans (Mahon and Smith, 1989). Likewise, multistock models, as is evident for haddock in the northwest Atlantic, should be developed and applied in a similar context to multispecies models. Conceptually, species and stocks can be viewed as the same unit or level of hierarchy in these models, although by definition of a species, more gene flow would be expected between stocks of the same species than between species, but treatment of the two units could be the same.

Stock structure information provides a basis for understanding the dynamics of fish populations that assists scientists and managers in predicting how a stock may respond to different management strategies. Investigation into the tempo-

[9] Begg, G. A., and J. R. Waldman. An holistic approach to fish stock identification. Manuscr. in review.

ral stability and historical shifts in stock structure of haddock throughout the northwest Atlantic via archived biological samples and data sets in relation to environmental fluctuations and effects of the fisheries, will enable an historical perspective of stock structure to be developed. This would assist in understanding the collapse of haddock stocks throughout their distribution and the implications of these effects to current stock assessment, rebuilding, and management plans. Consequently, identification of haddock stocks and their rates of mixing should continue to undergo investigation in order to refine our understanding of haddock stock structure in the northwest Atlantic.

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